Past and Present Limnological Investigations

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Abstract. The limnological investigations in Uganda freshwaters which were started in the 1920s looked into: the origins, the changing geological and climatic factors which gave rise to the characteristic inland waters; the primary production; the constituent small aquatic organisms and their ecology; and their bordering swamps. Most of them were formed immediately after the formation of the great Western rift valley.

Almost all the inland waters in Uganda are typical tropical freshwaters which, because of their relative shallowness, experience rather frequent wind stirrings and therefore nutrient circulation which would make them relatively productive. Many physical, biological and chemical factors come into play to finally determine this.

The present investigations continue to bridge the gaps which were left and also to collect the baseline data needed to later manage, monitor and control any possible pollution risks.

Introduction

Limnological investigations in Uganda started in the 1920's. They were mainly theoretical, seeking to unravel the history and origins, the changing environment, and the biology and ecology of some of its inland waters. The present, and more applied investigations, are geared to the answering of the day-to-day questions concerning the aquatic environment and its potential resources and to filling the gaps that were left in the original investigations.

In this overview are discussed the historical origin and forluation, freshwater environmental variable (chemical, physical and biological) and their ecology, primary productivity, aquatic organisms and communities, and studies of swamps that have been Inade.

The Historical Formation and Origin of the Ugandan Freshwaters

It was the earth movements which gave rise to the great rift which extends southwards fron1 the Dead Sea through Ethiopia to split into two branches, the Western Rift through Zaire, Uganda, Rwanda, Burundi, Tanzania, Zambia and Malawi, and the Eastern or Gregory rift (Gregory, 1896, 1921) through Kenya and Tanzania. great ridge, as a result, has run from Eritrea to the Zalnbezi river. This has raised a thousand or so n1etres since the lniocene era (about 20 ııı yrs ago). The centre of the East African section of this great ridge has sagged to form the enormous, though shallow basin of L. Victoria (Beadle, 1974; Livingstone and Melack, 1980).

The rifting was in general at right angles to the previous East-West drainage from the high ridge of Eastern Africa and the trenches so formed, whose floors are in places more than 1000 m below the tops of the bounding walls, have collected a great amount of water. Almost all of the Great Lakes of Eastern Africa have originated in this way, together with their major inflows.

The origin and past history of L. Victoria has been the subject of some controversy, since the pioneer geological work of Wayland (summarized in 1934). Much has been written on the subject in terms of the geology (Bishop, 1969); archaeology (Bishop and

Fig. 1. A physical map of Uganda showing the major inland waters.

Ponansky, 1960); climate and ecological history from the study of sediment (Kendall, 1969); for distribution and speciation of fish (Worthington, 1954; Gr wood, 1951a) and recent interpretation of combined geological and zoological evidence (Temple, 1969).

The dendritic shape of L. Kioga is due to the tectonic blockage of the Nile by th tilted shoulder of the Western and Gregory rifts, and has been locally deepened an extended by block faulting as well. It thus lies in the flooded branches of the old west-flowing Kafu River, and now receives the outflow from L. Victoria (the Victoria Nile) and drains northwards and falls over the low northern end of the right escarpment (the Murchison Falls) and thus to L. Albert and the Albert Nile.

Owing to a historical geological accident the overflow from Lakes Victoria and Kioga (the Victoria Nile) originated by uptilting of the Victoria basin in the late pleistocene era and made its way via a previous river valley to a low point along the rift wall to plunge over the Murchison Falls to reach Albert at its very northern most end, almost directly into the outflowing Albert Nile.

The disposition of Lakes George and Edward is peculiar, the former situated on a plain in a branch of the Rift Valley between the Kichwamba escarpment and Rwenzoris. Kazinga Channel connects it to L. Edward to which it flows.

Geological evidence suggests that L. Edward may only recently have overflowed by the Semliki route (Beadle, 1974). Previously, it appears that the upper section of the river may have flowed into L. Edward and was subsequently captured by cutting back of the lower section which flowed into L. Albert (de Heinzelin, 1955, 1963), which is a typical rift valley lying at an altitude of 615 m between two parallel escarpments. The main inflow is the R. Semliki from L. Edward, together with contribution from stream from the northern slopes of the Rwenzoris.

Presently, the fauna of L. Edward and L. Albert indicate some existence of conlmon species of fish, similar to those of L. Victoria, which is sonle further evidence that they were all connected, as recently as the pleistocene.

Volcanism associated with rifting has been a fertile source of African lakes. These lakes, in S.W. Uganda (Denny, 1972) were formed mostly by lava-damming of river valleys. The release of the earth's crust internal pressure by cracking has been accompanied by earthquakes and volcanic eruptions. In several places, volcanic explosions with or without the ejection of substantial amounts of volcanic ash, have created large numbers of small, round, often deep maar lakes at the foot of the Rwenzoris (Livingstone, 1967).

These upthrust fault blocks of the Precambrian rocks that lie across the western Rift, extend above the snowline or have done so during the pleistocene era, with attendant growth of glaciers and a formation of glacial lakes. Most of these lakes occupy glacial rock basins, commonly of the cirque or paternoster types (Coe, 1967). The glacial lakes are small and shallow. Small but numerous saline lakes are also scattered throughout the Western Rift. Analyses of sediment cores from Lakes Victoria and Albert indicated that alkaline water occupied these lake basins within the last 13000 years (Harvey, 1976; Kendall, 1969; Richardson and Richardson, 1972).

In the Virunga volcanic regions in the S. W. corner of Uganda, several lakes were formed during the late Pleistocene era (35000 yrs ago.) In this same volcanic region are a number of smaller lakes which have been formed in the same manner just outside the rift.

Environmental Variables and Primary Production

Climatic changes together with physico-chemical and biological variables have interacted to give rise to the present state of Uganda freshwaters. Serious study of past climates in tropical Africa, as revealed in exposed alluvial and lake sediments and raised beaches with their fossil and human artifacts, was started in the 1920s. There were great climatic fluctuations during the pleistocene era, especially in rainfall. A good account of the East African pre-history based on the dry-wet climate schemes, is to be found in Cole (1954).

A number of climatic factors interact to determine a given lake level, lake organic production, and lake budget. It is factors like the seasonal or diurnal wind pattern (which stirs and circulates the nutrients) which has determined the general rate of organic production and its seasonal fluctuations. The seasonal changes in the direction of the prevailing winds over the African continent indirectly affect its rate of primary organic production. The local diurnal wind breezes must make some contribution to the productivity of shallow or inshore waters by maintaining vertical circulation which ensures nutrient distribution. It is these different environmental variables which can be categorised into the chemical, physical and biological factors that have interacted in such ways as to give the different and characteristic aquatic ecosystems. All these are being looked at now with one prime objective, namely, the interaction of these variables to produce conditions required to maintain a permanently productive fishery, which is the practical objective of limnology.

TaIling and TaIling (1965) recorded and discussed the comparative ionic composition of lakewaters of Eastern Africa. The great differences in chemical composition exert a primary control on the distribution and abundance of organisms (La Barbera and Kilham, 1974; Hecky and Kilham, 1973; Talling and Talling, 1965).

In the Ugandan freshwaters it was found that bicarbonate was the major anion. The conductivity (total ionic concentration) and alkalinity varied widely due largely to saline inflows from volcanic areas and evaporation within basins of closed drainage. Variations in the proportions of the major anions were limited, although local enrichnlent in ions occurred. The proportion of S04 was particularly low in some lakes (Beauchamp, 1953) with de-oxygenated hypolimnia. In many lakes Na^+ was the principal cation and the monovalent cations often preponderate over the divalent.

The concentration of NO_3N was usually very low in lake surface waters, whereas amount of dissolved SiO_2 and total PO_4P were generally high. The major ionic composition of the lakes appeared to be similar to that expected from the combined contributions of the inflows. The Inajority of inflow, however, have not had a fair share of the limnological investigations. Many inflows from volcanic highlands have flowed to basins of internal drainage and generated salt lakes, and others from other types of highlands gave rise to different lakes of varying ionic composition. The very high alkalinities of Some Ugandan lakes have sometimes been attributed to chemical peculiarities of the volcanic rocks that surround many of them. The high concentrations of Na^+, HCO_3^- and CO_3^- of the closed lakes and also the accompanying pH of 10 or

Table 1. A few comparative limnological parameters for the major Ugandan freshwaters: (a) lakes (b) rivers.

a)

	Victoria	Edward	Albert	George	Kioga
Conductivity MS. cm^{-1}	96	925	735	200	200
PH range	7.1-8.5	8.8-9.1	8.9-9.5	8.5-10.0	7.4-8.5
Approx. salinity	0.093	0.789	0.597	0.139	
Na^{+} meq. 1-1	0.430	4.78	3.96	0.59	0.47
K^{+} meq. 1-1	0.095	2.32	1.67	0.09	0.27
Ca^{2+} meq. 1-1	0.280	0.57	0.49	1.00	0.54
Mg^{2+} meq. 1-1	0.211	3.98	2.69	0.67	0.57
$CO_3^{=}$ meq. 1-1	0.900	9.85	7.33	1.91	1.17
$SO_4^{=}$ meq. 1-1	0.037	0.89	0.76	0.23	0.65
NO_3 N ppm	1.32	1.40	0.009	1.45	0.02
PO_4P ppm	0.9	0.25	0.13	0.50	0.20
SiO_2 ppm	3.9	6.0	3.4	11.5	34.0

b)

	Victoria Nile	Kagera	Semliki
Conductivity MS. cm^{-1}	130	100	500
$HCO_3 + CO_3$ meq. 1-1		0.86	7.3
SO_4 ppm	1.5		36.4
Ca^{2+} ppnl	7	5.4	15
SiO_2 ppm	2.5	17	3.8

more, is the result of evaporative concentration with selected removal or less soluble salts (Arad and Morton, 1969).

River and rainfall inputs (Visser,]961, 1964b; Ganf and Viner, 1973) of the nutrients into the lakes cannot be overstressed. Many river analyses have been provided for Africa by Kilham (1971a), Pittwell (1971) and especially by Viner (1975) who wa concerned specifically with nutrient flux. Most of this information, however, is not based on the long series of repeated samples extending over several years that are needed to draw up accurate nutrient budgets (Likens et aI., 1977).

Of the individual Ugandan freshwaters, it is L. George, which so far, is the most studied by the IBP team and by individual workers or department (Viner, 1969; Burgis et aI., 1973; Ganf and Viner, 1973; Gwahaba, 1973; Moriarty et aI., 1973; Viner and Smith, 1973; Ganf, 1974a-d, 1975; Burgis, 1974,1978; Greenwood, 1976; Viner, 1975c, 1976, 1977; Bugenyi, 1979). Complete budgets for N and P for this lake have been provided, although it still lacks detailed estimates of inputs from rain and rivers.

Regeneration of nutrients by zooplankton has been studied also at L. George, using the very small abundant cyclopoid, which dominated the zooplankton assemblage during the study (Ganf and Blazka, 1974.)

L. Edward, is not exposed to powerful winds and therefore is not fully circulated annually and experiences some kind of stratification. Its profile is peculiar in that, though about 40 km wide, the deepest water (112 m) lies within 4 km of the Zaire shore where the western escarpment falls precipitously into and under the water. Below 50 to 60 m there is normally no oxygen (Beadle, 1932b, 1932; Damas, 1937), and the stagnant anoxic layer which is highly reducing with free H_2S is thus confined to a trench along the western shore. More than two-thirds of the lake is less than 50 m and is frequently stirred and always oxygenated to the bottom.

L. Albert is an example of a large tropical lake which was not originally thought to develop a vertical stratification nor to show marked seasonal changes in circulation owing to its shallow depth (max. 55 m) relative to the other large Rift Valley lakes and the violence of the winds blowing along the deep trench-like valley (Worthington, 1929; Verbeke, 1957a). Nevertheless, Talling and Talling (1963) has shown from measurements of temperature, oxygen and other chemical constituents that thermal and chemical gradients develop, but without a marked thermocline, during the calmer periods of the year.

L. Victoria, which is relatively shallow, has been said to experience cycles of stratification as determined by the seasonal wind pattern (Talling, 1964; Kitaka, 1971). The first fisheries survey of the lake in 1926-27 by Graham (1929) provided evidence of both temperature stratification and homothermal conditions in different regions. It was in L. Victoria, however, in 1952-53 that the first clear evidence of a regular seasonal cycle in a tropical lake was found by Fish (1957). It was since been confirmed by others (Newell, 1960, Talling 1957b, 1964, 1969) and is now recognized as a characteristic feature of several other large lakes in tropical Africa.

It is only in Lakes George (Ganf, 1969) and Victoria (Talling, 1965b) that sufficient measurements have been made for over a year to justify calculation of an integrated annual figure for photosynthetic production and to demonstrate quantitatively an absence of seasonal change. Gross primary production is seasonally limited by low temperature or low intensity or radiation. The main controlling factor is the nutrients (and thereafter their circulation by the internal waves caused by the winds). For the deeper, large open lakes (like L. Victoria), the nutrients are locked up during some calmer seasons as a result of thermal stratification. L. Victoria is stirred by trade winds circulating the nutrients, and this leads to high blooms and hence a high primary production rate (Fish, 1956, 1957; Talling, 1957b, 1965). Studies in that lake (Talling, (1966) and in the White and Blue Nile Rivers (Prowse and Talling, 1958; Talling and Rzoska, 1967) indicated that the nitrate frequently may limit algal growth.

The factors which appear to determine the upper limit of production rate for tropical lakes are:

(i) The rates at which nutrients are released from the mud (Kamp-Nielsen, 1979) and from organisms throughout the water column.

(ii) The increases in density of phytoplankton through growth, which tends to limit photosynthesis by reducing the depth of the euphotic zone.

(iii) As the result of phytosynthesis, the dissolved oxygen rises during the day and the oxygen super-saturation acts as a partical inhibitor of photosynthesis.

Primary production benefits organisms in the higher trophic levels, in the long run. However, detailed information on transfer of nutrients and calories to higher levels in the food chains is very scarce. There are few data (Green 1967) for assessing fluxes to the fishes from lower trophic levels, through the fishes, or them to consumers other than man.

The Aquatic Organism Community

here has been both faunistic and geochemical connections of the freshwaters by fauna and flora movements through the rather flat flooded-water-sheds systems which provided a continuous sheet of water. The organisms could survive even in temporary water basins or in droughts by production of resistant spores. Thus, through immigration from elsewhere and through the production of new species in situ, this ensured the continuous speciation over the years. Work on speciation in the East African lakes can be found in Beadle (1962), Lowe-McConnel (1969), and Fryer and lIes (1972).

It is generally true that the few species that finally manage to adapt to extreme conditions and thus survive, are little hampered by competition and are often extremely numerous. In the context of competition and other ecological aspects, much work has been done on the invertebrates (Green, 1967, 1971; Verbeke, 1957a; Damas, 1937; and Burgis, 1969, 1970, 1971b). This, together with the works of Worthingtone (1929), Verbeke (1969), Hamblyn (1966) and Holden (1967, 1970), indicated that most of the available ecological niches are now occupied and that the resources of the lake are now a basis for productive fishery (Cadwalladr and Stoneman, 1968). The existence of some common invertebrate and fish species in the two lakes and in L. Victoria is evidence to show that they were all joined as recently as the late Pleistocene era. Considerable work has been done in L. Victoria invertebrates and other related ecological aspects (Macdonald, 1953, 1956; Corbet, 1958; Hartland-Rowe; 1958; Fryer, 1959d; and Tjonneland, 1958a and b).

Swamps

Many Ugandan lakes are bordered by highly productive wet-lands, the swamps (Beadle, 1932a; Carter, 1955; Gaudet, 1977; Lind and Visser, 1963; Thompson, 1976). There are also extensive swampy areas, not connected to any lake. The total swampy area in Uganda is said to be 6 % of the total surface area of Uganda (Lind, 1956).

Lakes bordered by papyrus swamps are economically important (Haward-Williams and Gaudet, 1976) in providing fish and water for: drinking, irrigation and sewage disposal. Although swamp fishing techniques are still inefficient, about 36 % of the African freshwater fish-catch is from swamps and flood plains (Welcomme, 1972). Some of the lakes bordered by swamps provide the most productive fishery, e.g., L. George. An understanding of the nutrient relations which determine the fishery productivity of a lake between swamp and lake is a specific and very difficult problem of African limnology.

Water Environments through the rooted and floating swamps have a marked effect on dissolved gases and nutrient levels. The dissolved gases of most importance to the ecology of tropical swamps are oxygen, carbon dioxide, methane, nitrogen and hydrogen sulphide.

There is little evidence that methane or any gas other than O_2 and CO_2 has any great influence on the aquatic life in tropical swamps (Beadle, 1974). Dissolved CO_2 is comparatively high in swamps and is greatly influenced by flow-through, giving rise to a low pH (Carter, 1955; Beadle, 1974). DIssolved H_2S is seldom encountered in tropical swamps. Occasional areas of intense decomposition in the Ugandan papyru swamps were shown to result in methane (Carter 1955).

Nitrogen gas is readily available to the swamp N-fixers. The major portion of nitrogen compounds in the swamp must come from N-fixation, so the proportion of imported N-compounds in a papyrus swamp nutrient. budget mut be very small.

Thus, the waters flowing through these swamps are in Some way altered. The evidence available indicates that the major factor influencing the chemical composition of the flow-through is the rate of flow. Viner (1970) suggested that papyrus swamps around L. George had little effect, because of the high rate of flow through. When the rate is slow, the swamps are said to trap (by organic sediulentation) the ions.

This can be advantageous, however, in that the swamp systems can be used to control pollution. They are able to remove not only Nand P from flowing waters but also pathogenic bacteria of faecal origin and mineral nutrient pollutants from a variety of diverse sources. Unfortunately, swamps are often associated with diseases such as schistosomiasis and malaria. The present day investigations (Bugenyi, 1977, 1980, unpublished) are geared to finding the baseline data on these freshwaters which can be used for managelnent and later for pollution control purposes. The prime objective is the conservation of aquatic resources.

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